THE NEW VIEWS ABOUT REVERSION.

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To the general principle that "like begets like" striking exceptions are not infrequently found. These exceptional cases fall into two classes. In the one class the child possesses some character not visible in either parent but found in a grandparent *e. g.,* blue iris in the chlidren of brown-eyed parents. This is known as *atavism.* In the other class, the child possesses some character not visible in immediate relatives but found in some remote ancestor or even ancestral species; *e. g.,* the reappearance of the Jungle fowl plumage among domesticated poultry. This is known as *reversion.*

Of these two phenomena reversion is the more striking and the explanation that has been current until recently, even among biologists, and is still common among breeders is essentially that of Darwin[1]—"An inherent tendency to reversion is evolved through some disturbance in the organization caused by the act of crossing."

The new explanation is based on the principle that the unit of inheritance is not the individual but some *characteristic* of an organism. Paternal or maternal characteristics are not inherited en masse for the most part but each character independently of every other. A second principle, no less important, is that inheritance is not truly from the parents but from the germ plasm; it is not the adult characters that are inherited but something in the germ cells that will eventually determine those characters. One may dispute the hypothesis of pre-formation in the germ but one can not deny that the egg of an ox is predetermined, certain conditions being fulfilled, to develop into an ox while the egg of man is similarly predetermined to develop into a man. There are probably numerous points of difference in the minute chemical structures of these

[1] Variation of Animals and Plants under Domestication," Chapter XIII.

two eggs and these differences determine the different end results. They may be called *determiners*. Ordinarily, when parents are similar, each unit character of the offspring develops from two similar determiners—one paternal and one maternal. Thus in its origin any unit character is duplex. When, however, the determiner is found in only one of the parents the character is simplex. Now such a character frequently develops imperfectly because of the partial stimulus to development.

If in an individual any character is simplex then the germ cells of that individual are typically of two kinds; half have the determiner for the character and half lack such determiner. Now if two such individuals be parents the chances of the uniting of (*a*) two germ cells with the determiner, (*b*) two germ cells without the determiner, and (*c*) one with and one without are as 1 : 1 : 2, or 25 per cent. of the offspring will have the character duplex; 50 per cent. will have it simplex, while 25 per cent. will lack the character —and will thus resemble one of the grandparents!

To illustrate: If the two grandfathers have blue eyes and both grandmothers brown eyes then the parents may both have simplex brown eyes; they will both form germ cells of which 50 per cent. have and 50 per cent. lack the determiner to form brown iris pigment. From such brown-eyed parents one child in four will have blue eyes like the grandfathers. This is atavism. Cases of atavism can, in general, be explained on the same ground as atavism to blue-eyed grandparents. Complications are indeed induced by sex-limited heredity, illustrated by the horns of sheep which appear, when simplex, only in males of certain strains. A further complication is seen in cases of apparent or partial blending as in human skin color. But in the great majority of cases atavism is a simple reappearance in one fourth of the offspring of the absence of a character due to the simplex nature of the character in both parents.

Reversion in the strict sense has a more complicated explanation. It depends in general on the circumstance that many apparently simple organs or color patterns or colors are really complex and require the coöperation of two or more elementary characteristics called *factors*. For generations a particular character may

not appear but when two parents together produce the required factors the combination may be an apparently new, compound character; which we find elsewhere only in remote ancestry.

The facts of reversion are most notorious among domesticated animals and plants. The reason is that man has preserved just those strains of germ plasm that are peculiar in the absence of some typical characteristic or the presence of some new characteristic. These new conditions either cause the ancestral condition to fail of development or mask it over. In hybridizing we restore the factor that is missing from one strain by introducing it from another strain; or we remove the added factor that veils the ancestral condition. Thus the ancestral condition is restored—a reversion occurs.

The foregoing general statement may now be illustrated by some examples.[2] The goldfinch, which has plain chestnut sides, when crossed with a plain yellow canary produced hybrids that have stripes on back and flanks. Darwin mentions this case[3] and adds: "this streaking must be derived from the original wild canary." The results of breeding indicate that the yellow canary has one factor for these stripes—as it were, the potential pattern—but no pigment to bring it out. Adding the factor of pigment from the goldfinch the pattern appears in the offspring.

Reversion in poultry was studied by Darwin. He crossed a White Silkie hen with a Spanish cock which is perfectly black except for the iridescent glossy black in hackle, saddle, wing bar and some of the tail feathers. "As the cocks grew old one . . . became a gorgeous bird. When stalking about it closely resembled the wild *Gallus bankiva,* but with the red feathers rather darker." The hens were black. I have made the same cross with the same result. Moreover, when the hybrids were mated together some of the females as well as males assumed a perfectly typical Jungle fowl coloration. The "reversion" was now complete.

The interpretation of this case on the factor hypothesis is some-

[2] The colored lantern slide illustrations are not here reproduced; they appear in part in the author's works entitled, "Inheritance in Poultry," "Inheritance in Canaries," and "Inheritance of Characteristics in Domestic Fowl," all published by the Carnegie Institution of Washington.

[3] Var. Dom. A. and P., Chap. XIII.

what complex but perfectly clear. All fowl except the booted races (which are of Asiatic origin and allied to the Aseel fowl) contain the determiner—complex for the Jungle fowl color pattern. We may call it J. This factor alone is impotent without a color-producing enzyme (C). The Silkie fowl apparently lacks this in the plumage and so remains colorless. The Spanish has it and so produces the Jungle pattern of which the red portion is nearly coincident with the glossy portion of the Spanish plumage. But the Spanish has an additional factor, an additional black coat (N), which turns the red part of the pattern black. Thus the Spanish color factors are CJN whereas those of the White Silkie are cJn, the small letters indicating the absence of the factors concerned. When the germ cells of the two races fuse the fertilized egg contains factors CcJ_2Nn; which means, the color enzyme is simplex, the Jungle pattern is duplex and the supermelanic factor is simplex. Since N is simplex it is insufficient to cover all of the red in the male, where it is strongest and so the males show some red, only, as Darwin says, it is darker than in the Jungle fowl. Now the germ cells of these hybrids have their characters all simplex: and they are consequently of four kinds: viz: CJN, CJn, cJN, cJn. If two such hybrids be mated their germ cells unite at random. If two germ cells of the first type unite a black bird results; if two of the second type Games result; if two of the other two types unite whites result. I reared 362 offspring from the hybrids; the relation of expected to observed birds of each type of color is shown on Table I.

TABLE I.

	Black.	White.	Game.
Expected	205	90	67
Observed	210	95	57

One sees that it is not hybridizing *per se* that produces the Game or Jungle coloration, else all would be so colored. It is the union of the requisite ancestral factors one or more of which are missing from the domesticated, fancy strains.

Again, if a White Silkie be crossed with a White Leghorn, the offspring are all white except that the males show some red in those parts of the plumage that are red in the Jungle fowl. In the second

generation some individuals, both males and females, show a typical Jungle fowl coloration. In this case the factors in the White Leghorn are the same as in the Black Spanish with the addition of another—the whitening factor (W), probably an antienzyme that stops the work of the pigmentation factors. Thus the formula of the White Leghorn is CJNW and its hybrids with the Silkie have the formula CcJ_2NnWw. The germ cells of the hybrids are of eight kinds, namely, CJNW, CJNw, CJnW, CJnw, cJNW, cJNw, cJnW, cJnw. These give 64 combinations in the fertilized eggs of the second hybrid generation. I raised only 85 chicks. The relation of expected and observed numbers is given in Table II. It will be seen that realization runs close to expectation.

Table II.

	White. (Including F_1 Type of Color.)	Game.	Black.
Expected	69	12	4
Observed	68	16	1

Finally, I may refer to a cross between the Black Cochin and the Buff Cochin. The Black Cochin has the color factor C and it has the supermelanic coat, but it seems to lack the red of the Jungle type of coloration. This modified Jungle type may be called I. The Buff Cochin is like the Black Cochin with the addition of a superxanthic coat (X) which produces the uniform red color. In the second hybrid generation these factors should appear in the combinations shown in Table III.

Table III.

1 $C_2I_2N_2X_2$ Black	2 $C_2IiN_2X_2$ Black	1 $C_2i_2N_2X_2$ Black
2 $C_2I_2N_2Xx$ Black	4 C_2IiN_2Xx Black	2 $C_2i_2N_2Xx$ Black
1 $C_2I_2N_2x_2$ Black	2 $C_2IiN_2x_2$ Black	1 $C_2i_2N_2x_2$ Black
2 $C_2I_2NnX_2$ Black and red	4 C_2IiNnX_2 Black and red	2 $C_2i_2NnX_2$ Black and red
4 C_2I_2NnXx Black	8 $C_2IiNnXx$ Black	4 C_2i_2NnXx Black
2 $C_2I_2Nnx_2$ Black	4 C_2IiNnx_2 Black	2 $C_2i_2Nnx_2$ Black
1 $C_2I_2n_2X_2$ Buff	2 $C_2Iin_2X_2$ Buff	1 $C_2i_2n_2X_2$ Buff
2 $C_2I_2n_2Xx$ Buff	4 C_2Iin_2Xx Buff	2 $C_2i_2n_2Xx$ Buff
1 $C_2I_2n_2x_2$ White	2 $C_2Iin_2x_2$ White	1 $C_2i_2n_2x_2$ White

each combination having the prefixed frequency and yielding the color indicated. Uniting black and black-and-reds, since red ap-

pears in one sex only and not until late in life, we get the relations between the calculated and observed proportions in 86 offspring shown in Table IV. Here again the observed distribution agrees with the hypothesis.

TABLE IV.

	Black and Black and Red.	Buff.	White.
Expected	65	16	5
Observed	61	17	8

We may conclude, then, that reversion is not due to the act of crossing in and of itself. It is rather due to the restoration of the ancestral factors, neither more nor fewer. The ancestral combination occurs in by no means all of the hybrids but only in a predictable proportion.

In conclusion, a suggestion may be offered as to the frequently observed fact of reversion to the ancestral coloration of domestic fowl which have become feral, as, *e. g.*, in the Hawaiian Islands. Darwin suggests that at least part of the reversion of the domesticated animals that have run wild must be due to the new conditions of life. One observation that I have made sheds some light on the question. When domestic races run wild much intermingling of races occurs and the primitive type of coloration, among others, recurs. When, as is usually the case, this is better fitted to survive because of inconspicuousness or other advantage, it will tend to escape the general slaughter. That selective elimination is real in poultry is shown by an experience of mine. In an open field about 300 chicks ran at large. About 40 per cent. of them were white, 40 per cent. black and 20 per cent. penciled or striped. Twenty-four were killed by crows—all either solid white or solid black except one that was coarsely mottled gray and buff. It is obvious that the self-colored poultry are at a disadvantage because of their greater conspicuousness, and they must be, in time, eliminated, leaving only the striped or penciled birds—those of the ancestral type of color. Reversion is here not a germinal but an environmental result, due, however, not to climate but to organic enemies.